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Earthworm-amended soil structure: Its influence on Collembola populations in grassland

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With 2 figures

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1. Introduction

Soil structure is known to affect soil biota. The effect can be indirect, via the influence of soil structure on flow of air and water through the soil, and on soil temperature. But, soil structure is also important because it provides the soil biota "living space" and shelter against abiotic stress and predators. Soil macrofauna are often able to modify the spatial characteristics of soil structure, but the meso- and microfauna and the microflora are not. An example of how soil structure affects the functioning of soil meso- and microfauna is given by the experiments of Elliott *et al.* (1980) with fine and coarse textured soil. They showed that nematodes could not reach their food (Bacteria) as well in the small pores of fine textured soil, while the much smaller amoebae in the same experiment were less affected by pore size.

In view of the importance of pores for soil animals, particular attention should be paid to characterizing the pore system of the soil. This can be done in several ways. The total pore volume of a soil can be measured relatively easily, and has been correlated with size of mesofauna individuals. A more detailed way to look at pores is to measure the pore size distribution. This can be done by physical analysis of undisturbed soil cores (*p*F-measurements), but also by studying soil thin sections. Thin sections have the advantage that the architecture of the pores, that is the form and interconnection of the pores, can also be studied. Darbyshire *et al.* (1985) tested different methods to analyze pore size distribution in thin sections, and discussed the potential of this method in ecological studies of Protozoa. Unfortunately they made no measurements on the protozoan fauna itself. Haarløv (1955, 1960) made sections of agar-embedded soil and found a reasonably good correlation between number of small pores and the distribution of small Collembola species.

Earthworms influence, the soil structure by channeling and mixing the soil with organic matter, thereby increasing pore volume and creating a more aggregated structure. In a soil with high earthworm-activity soil aggregates are rounded and porous with a heterogeneous pore size distribution. Therefore such soils have larger pores and a higher pore volume than a comparable soil without earthworms. A study of soils with and without earthworms can shed light on the relationship between pore structure and living possibilities for soil biota that are unable to modify the soil structure themselves.

Some of the most recent Dutch polders were reclaimed from an inland sea between 1945 and 1960. These extensive areas of fertile, mostly loamy soils, are isolated from the main land by shallow water. The land is only partly colonized by earthworms. At some sites earthworms have been introduced deliberately. After 10 to 25 years, earthworm populations are still restricted to areas close to the sites of introduction. Therefore these locations provide experimental plots with and without earthworms, close together, that are under the same type of land use. Clear differences in the soil structure can be ascribed to earthworm activity (Hoogerkamp *et al.*, 1983).

In this work we tried to quantify the influence of the 2 types of soil structure on number, species composition and size of Collembola. Collembola were chosen because they can be seen as a representative for the fauna that is not able to change soil structure. Also, large numbers of both species and individuals of Collembola are often present in pasture soils.

2. Materials and methods

2.1. Site

The site of the study is a pasture area near Swifterband in the dutch polder Oostelijk Flevoland, which was reclaimed in 1957. Earthworms were inoculated locally in 1971 and 1972. The pasture is used for dairy farming with a stocking rate of 3–4 cattle units per ha. The fields receive a yearly dressing of 330–550 kg N per ha. The pasture is alternatively used for grazing and hay-making. The parent material of the soil is a stratified silt loam deposit of lacustrine origin. The carbonate content in the upper 50 cm is 7.7 to 11.1%, organic matter contents (loss on ignition) vary from 2.1 to 4.6%, and *p*H (KCl) is 7.1 to 7.5. The upper 20–30 cm has been mixed by ploughing shortly after reclamation. The soil is artificially drained by ditches and tile drains. Groundwater levels are within 100 cm of the surface. The soil is classified as an aeric Fluvalent (Soil Conservation Service, 1975) or a calcaric Fluvisol (FAO/UNESCO, 1974). Earthworm populations consist of *Aporrectodea caliginosa* (78%), *A. longa* (11%), *A. rosea* (1.5%), *Lumbricus rubellus* (8%) and *L. terrestris* (0.7%), with a population size (1979) of around 200 per m^2 (HOOGERKAMP *et al.* 1983).

In the absence of earthworms, dead and decaying organic matter accumulates on the surface of the mineral soil forming an O-horizon of 2–2.5 cm thickness. The transition to the mineral soil is abrupt. In the mineral material, the only signs of soil formation are a system of cracks and fine grass-root channels down to the groundwater levels, with grey mottling along these voids. In the presence of earthworms a dark A_1 horizon starts to develop to a depth of 6–8 cm. Through time, this horizon thickens, and the colour becomes darker. A second result of the channeling of the soil and casting by the earthworms, is that the weak plate-like or moderate block-like structure of the upper decimetre becomes granular. Conductivity for water at saturation and for air at *p*F-2 are higher in the upper 20 cm of the soil containing earthworms. In deeper layers, the number of channels observed were invariably low. Dry matter yields of the grass (6 cuts) in 1981 were 10% higher in fields with earthworms, mainly caused by higher yields in spring and autumn cuts. (All from HOOGERKAMP *et al.*, 1983).

2.2. Sampling

Sampling of soils and mesofauna was done on the 20th of May, 1984. 2 adjacent fields, one with and one without earthworms, were sampled. 10 samples per field were taken by means of a soil corer (internal diameter 5 cm) to a depth of 5 cm. The soil core was divided in 2 layers, 0–2.5 and 2.5–5 cm from the surface. The Collembola were extrated using a modified Tullgren-apparatus. Temperature was raised gradually from 15 °C to 40 °C over 4 d. The sampling vessels were water-cooled to provide a maximum temperature gradient, and contained a saturated solution of picric acid. After extraction, Collembola were transferred to microscopic slides with a slight depression in the centre, filled with Gisin-solution (GISIN, 1960), allowing the manipulation of the animals by gently moving the cover-glass.

For the preparation of thin sections, two soil samples, 5 cm high, 8 cm wide and 13 cm long were taken from each field. The water in the samples was replaced by acetone to avoid shrinking of the material, and the samples were embedded in polyester resin (MIEDEMA *et al.*, 1974). After hardening, 2 vertical thin sections per sample were prepared, 5 cm high and 8 cm wide, resulting in 4 thin sections per field.

2.3. Measurements

Collembola were determined to genus-level, and if possible to species-level. The length of each individual was measured from the forehead to the end of the sixth abdominal segment, along the median axis. The width is probably important in determining the accessibility of the individual animals to pores, but is difficult to measure, because the soft collembolan bodies are easily distorted under the pressure of the glass lid.

Pores were described qualitatively and quantitatively from the thin sections. Quantitative observations were made with a Quantimet electro-optical apparatus on photographs of the thin sections. The photographs were taken under a polarizing microscope to distinguish voids from crystal grains according to ISMAIL (1975). Total pore space of the two soil layers was assessed. Also, the cross-sectional area and the perimeter of each individual pore was measured. Using transects across pores in eight different directions, diameter values for pores were established. Of these eight, the smallest chord diameter, termed "width", was selected for further analysis. From the measurements of pore-width a pore size distribution was made, for which the size classes were chosen in concurrence with physical aspects of pore size and the size classes of Collembola. This pore-size distribution could not be made for the organic upper layer in the plot without worms, where only the 1.5–2.5 cm core was taken into account.

2.4. Statistical analysis

The numbers and lengths of Collembola found in the different layers and treatments were analyzed statistically. Because the numbers are not normally distributed, and the comparison of lengths is based on different numbers of animals measured per sample, the Kruskall-Wallis rank test was chosen to test significance between both number and length. A correction was made for ties[1]). No analysis was made of the results of pore size distribution because the number of replicates was only four.

3. Results

3.1. Micromorphology

Although both soil profiles must have been similar originally, current differences are clearly visible from the thin sections (see fig. 1). In the plot without earthworms, a 2–3 cm root mat is present. The root mat contains horizontally oriented easily recognizable plant remains, with a mix of moder-humus in the form of fecal pellets in between. Considering the quantity of fecal pellets and the presence of mineral soil particles, the root mat can be divided in two sub-layers; one mainly consisting of horizontally oriented dead grass shoots (0–1.5 cm), and one (1.5–2.5 cm) consisting of a concentration of fecal pellets and dead and living roots. Fungal hyphae can be detected in the root mat. The mineral layer under the mat is a mixture of coarse skeleton grains and big, rounded clay plasma balls, often with a clear unistrial orientation. It contains large shell remains. The original sedimentary layering, including thin organic layers, is still clearly recognizable. The pores in the mineral layer are mostly horizontally oriented joint planes[2]) with a diameter between 0.05 and 0.3 mm. Some vughs[3]) and vertical channels are present. The pores of the root mat consist mostly of interconnected vughs and planes.

In the earthworm plot, no root mat is present. The sections show a homogeneous mixture of skeleton grains and plasma. There is no sedimentary layering left, and also the unistrial plasma balls are absent. Shell remains are much smaller. Earthworm channels, chambers and aggrotubules[4]) are numerous. Plant remain in different stages of decomposition are evenly distributed through the soil profile. The pores consist of partly interconnected vughs and channels of various sizes.

The pore size distribution is given in table 1 A and 1 B. Considering the fact that the root mat is a habitat that differs from the mineral soil, it is better to compare the pore-system of the 2.5–4.5 cm layer in the plot without earthworms with the surface layer of the worm plot, and treat the root mat separately. Total pore space is lowest in the mineral layer of the plot without worms. In the earthworm plot pore space is higher and the two depth layers are very similar. The root mat in the plot without earthworms shows the highest pore space, caused by the loose packing of the grass litter in the root mat.

In the fecal part of the root mat the majority of pores measure 30–300 μm. In the mineral parts of both soil profiles the majority of pores (78–90 %) have a width smaller than 300 μm. The total number of pores is higher in the mineral layer of the plot without earthworms, mostly as a result of high numbers of pores smaller than 0.3 mm. The proportion of 0.3–1 mm pores in all mineral layers is about equal. Pores between 1.6 and 3 mm are more numerous in the earthworm plot than in the other. Although pores larger than 1.6 mm are not very numerous, they represent the largest part of the total pore space in both plots (more than 70 % in the worm plot and 25–40 % in the other). Pores >3 mm are only present in the earthworm plot.

Differences in pore size distribution between plots are smaller than expected, but it should be kept in mind that the smallest diameter (called width) is used for the size class distribution. This means, for example, that the big, irregularly formed earthworm channels that can be seen in fig. 1 B often are recorded in a relatively small width class. The mean size per pore for the different pore size classes (see table 1 C) gives support for this idea. The mean area per pore is the highest in the worm plot, mainly caused by the pores bigger than 1.6 mm. The activities of earthworms apparently cause a more aggregated structure with irregular and rather big pores in between. Within the aggregates, however, the matrix is compacted in comparison with the matrix in the soil without earthworms.

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[1]) Ties: more than one value identical within a treatment, causing disturbance in the assigning of ranks.
[2]) Planes: pores with parallel oriented walls.
[3]) Vughs: irregularly formed pores without orientation.
[4]) Aggrotubule: channel filled with aggregates, mostly excrement.

Table 1 A. Frequency distribution of pores per width class

pore width class [μm]	% of total pore number per width class			
	without worms 1.5–2.5 cm	without worms 2.5–5 cm	with worms 0–2.5 cm	with worms 2.5–5 cm
<30	18.5	43.2	11.4	8.2
30–300	64.0	46.5	71.6	69.4
300–420	5.6	4.3	6.6	6.8
420–540	3.5	2.1	2.9	3.6
540–660	2.5	1.1	1.8	2.1
660–780	1.1	0.9	0.0	1.7
780–900	1.0	0.6	0.8	0.8
900–1,020	0.7	0.4	0.8	0.6
1,020–1,620	1.9	0.7	1.5	1.4
>1,620	1.0	0.3	2.7	1.9
total number of pores	683	805	232	204

Note: Average of measurements on four thin sections of 5 cm × 8 cm.

Table 1 B. Frequency distribution of pore space occupied per width class

pore width class [μm]	% of total pore space per width class			
	without worms 1.5–2.5 cm	without worms 2.5–5 cm	with worms 0–2.5 cm	with worms 2.5–5 cm
<30	0.0	0.2	0.0	0.0
30–300	12.6	17.9	5.3	6.9
300–420	5.8	9.4	2.8	3.1
420–540	5.9	9.0	2.3	2.9
540–660	6.6	6.4	2.2	2.9
660–780	3.8	7.8	1.4	3.0
780–900	4.3	5.3	1.3	2.2
900–1,020	4.5	4.1	1.7	2.1
1,020–1,620	15.3	14.1	6.2	5.5
>1,620	41.2	25.5	76.3	70.2
total pore area [mm^2]	83.3	44.4	68.4	52.2

Note: Average of measurements on four thin sections of 5 cm × 8 cm.

Table 1 C. Mean area of pores in different size classes

pore width class [μm]	mean area per pore per width class (in μm^2)			
	without worms 1.5–2.5 cm	without worms 2.5–5 cm	with worms 0–2.5 cm	with worms 2.5–5 cm
<30	0.00	0.00	0.00	0.00
30–300	0.02	0.02	0.02	0.03
300–420	0.13	0.13	0.13	0.13
420–540	0.21	0.22	0.23	0.19
540–660	0.33	0.36	0.38	0.34
660–780	0.40	0.48	0.32	0.39
780–900	0.41	0.57	0.56	0.58
900–1,020	0.72	0.74	0.60	0.55
1,020–1,620	1.00	1.24	1.26	0.98
>1,620	4.48	3.02	7.57	8.81
all pores	0.06	0.06	0.28	0.26

Note: Average of measurements on four thin sections of 5 cm × 8 cm.

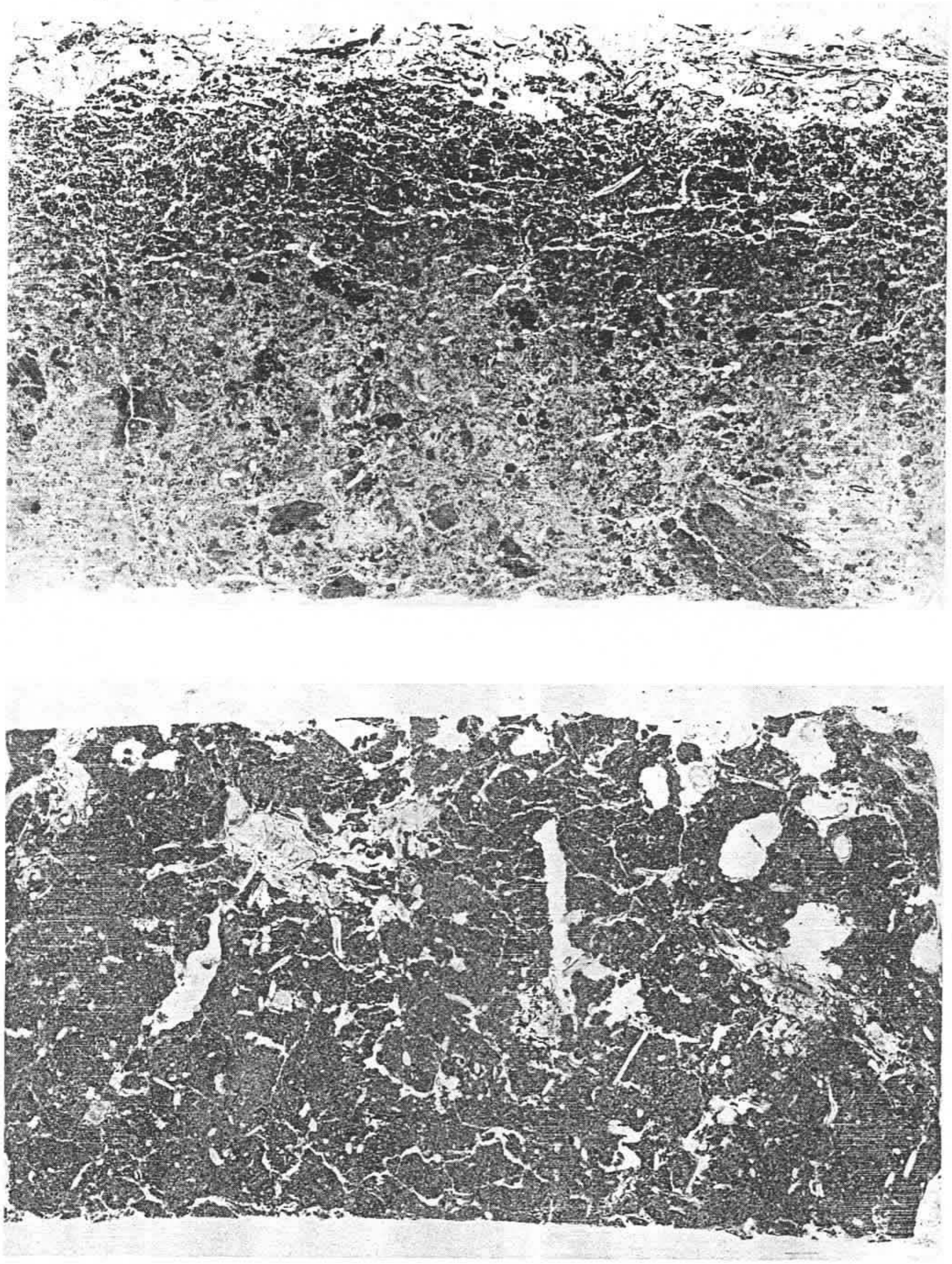

Fig. 1. Photograph of thin sections of (A) field without worms, and (B) field with worms. Size of sections 5 cm × 8 cm.

3.2. Collembola

Although the number of Collembola found was normal for grassland situations, the number of species was rather low (personal communication VAN DE BUNT). This may be because the rather young polders have not been invaded yet by all species. Seven genera were present, most of them represented by only one species. Species are listed in table 2, while the total number of individuals found in 10 samples are given in table 3. In both plots, there are no statistically significant differences between the numbers of Collembola in the two layers because of the high abundance of *Tullbergia* in both depth layers. *Isotoma, Proisotoma* and *Cryptopygus* are almost absent in the

Table 2. List of species found and some of their features

Name	Important features					
	F[1]	E[2]	P[3]	L[4]	H[5]	P[6]
Anurophorus boerneri (STACH 1922)	−	−	+	s	−	−
Cryptopygus bipunctatus (AXELSON, 1903)	+	1	+	1	+	−
Hypogastrura cf. succinea (GISIN, 1949)		6−8	?	s	++	+
Isotoma notabilis (SCHÄFFER, 1896)	+	3−4	+	1	+	
Lepidocyrtus ruber (SCHÖTT, 1902)	+	8	−	1	++	++
Proisotoma cf. minuta (TULLBERG)	+	8	+	L	+	
Tullbergia krausbaueri (BÖRNER, 1901) s.l.	−	−	+	s	−	−

[1] Furca. −: absent, +: normal length, : short
[2] Eyes (number of eye pairs)
[3] PAO (= post antennal organ). +: present, −: absent, ?: unknown
[4] Legs (can be long or short)
[5] Hairs. −: absent, +: normal, ++: very hairy
[6] Pigmentation. −: unpigmented, : slightly pigmented, +: pigmented, ++: heavily pigmented.

Table 3. Number of Collembola found in plots with and without earthworms

species	number of Collembola per 10 samples			
	w−, 0−2.5 cm	w−, 2.5−5 cm	w+, 0−2.5 cm	w+, 2.5−5 cm
Tullbergia k.	118	159	147	232
Isotoma n.	36a	1b	17a	14a
Proisotoma sp.	52a	−b	24a	146a
Cryptopygus b.	24a	1b	1b	8b
Anurophorus b.	5−	0−	0−	0−
Lepidocyrtus r.	0−	0−	6−	9−
Hypogastrura a.	0−	0−	3−	4−
Total	235	161	198	413

Note: Within rows, means followed by different letters are significantly different (Kruskal-Wallis, 0.05 level); not determined (−).

2.5−5 cm layer in the plot without earthworms, while *Proisotoma* is very numerous in this layer in the earthworm plot. Total numbers do not differ statistically between the plots. Some rare species only occur in plots without worms *(Anurophorus)*, others only in worm plots *(Lepidocyrtus* and *Hypogastrura)*.

The size distribution of the Collembola is given in fig. 2, and their mean size in table 4. Collembola clearly differ in size between both plots. Differences exist not only as a result of different species composition, but also because of size differences within species. The smallest size range is found in the deepest layer of the plot without earthworms, the biggest animals are found in the surface layer of the earthworm plot. Species that occur in the surface layers of both plots (mainly *Tullbergia, Isotoma* and *Proisotoma*) show a wider size range in the plot with earthworms. All species have a statistically significant higher mean length in the worm plot, and are also longer in the upper layer of this plot than in the layer 2.5−5 cm. The relatively big species of *Hypogastrura* and *Lepidocyrtus* are only found in worm plots.

Table 4. Mean length of Collembola species in plots with and without earthworms

species	mean length			
	w − d1	w − d2	w + d1	w + d2
Tullbergia k.	420.3 a	474.0 a	535.9 b	502.2 c
Isotoma n.	599.0 a	0	952.8 b	696.0 c
Proisotoma sp.	493.9 a	0	588.6 b	474.6 a
Cryptopygus b.	335.7 a	0	0 −	392.9 b
Anurophorus b.	282.0 −	0 −	0 −	0 −
Lepidocyrtus r.	0 −	0 −	1,368.6 −	555.9 −
Hypogastrura a.	0 −	0 −	849.3 −	484.0 −
Total	488.9 a	475.6 a	617.7 b	521.4 c

Note: Within rows, means followed by different letters are significantly different (Kruskal-Wallis, 0.05 level); not determined (−).

The figures in table 3 and 4 suggest that there are three different subgroups of Collembola that differ in number, size and species composition. These groups correspond to the populations in each of the 2 layers of the plot without earthworms, and in the earthworm plot as a total. These differences seem to be related to the pore size distribution (table 1), which also indicates much smaller differences between the 2 layers of the earthworm plot, than between corresponding layers in the non-earthworm soil. Unfortunately, the layers were not separated exactly at the transition from the litter layer to the mineral soil in the non-earthworm plot in both Collembola sampling and pore size measurements. Sampling in that way would probably have given a more precise characterization of the environment the different Collembola species prefer.

4. Discussion

Total pore volume of a soil has been shown to often give a correlation with size of mesofauna individuals. For example KLIMA (1956) noticed that deeper in soil profiles, both total pore volume and individual size of Collembola species decreased. HÅGVAR (1983) found that in woodland soils which had a relatively high pore volume in deeper layers also had higher collembolan densities than soils with a more compacted subsoil. In soils compacted by trampling, a reduction in pore volume coincided with a decline in population density of almost all soil fauna groups (CHAPPELL *et al.*, 1971). Factors other than pore volume may have been involved, however, because the vegetation and the organic profile of the soil had also changed under trampling. NAGLITSCH (1963) found much higher collembolan population densities in sandy soils than in clay soils, and also attributed this to the higher pore volume of sandy soils. However, some clay soils had a total pore volume which was equal to the pore content of the sandy soils, but still had a much lower population density of Collembola. NAGLITSCH supposed that the proportion of air-filled pores is much higher in sandy soils than in more finely textured soils with the same total pore volume. This implies that pore size distribution may be more important than total pore volume in determining living possibilities for mesofauna.

In this study, lengths of Collembola lay between 0.3 and 1.7 mm for the earthworm plot and between 0.2 and 1.0 mm for the non-earthworm field, although in both plots most individuals are shorter than 0.8 mm. Plots with and without earthworms do not differ in number of pores or in pore area fraction with a diameter in this size range. Although the big pores are much larger than needed for the largest Collembola, in the worm plot, where bigger pores are present, the individual size of the Collembola is also increased. This is in accordance with the findings of WILLIAMS (1972) who studied the distribution of faunal components in relation to the interstitial space available in shell-gravel sediments. He found correlations between size of adults of almost all taxonomic groups present and pore space available in the sediment. However, the mechanism causing this relationship was not clear because the biggest individuals of certain taxonomic groups were still considerably

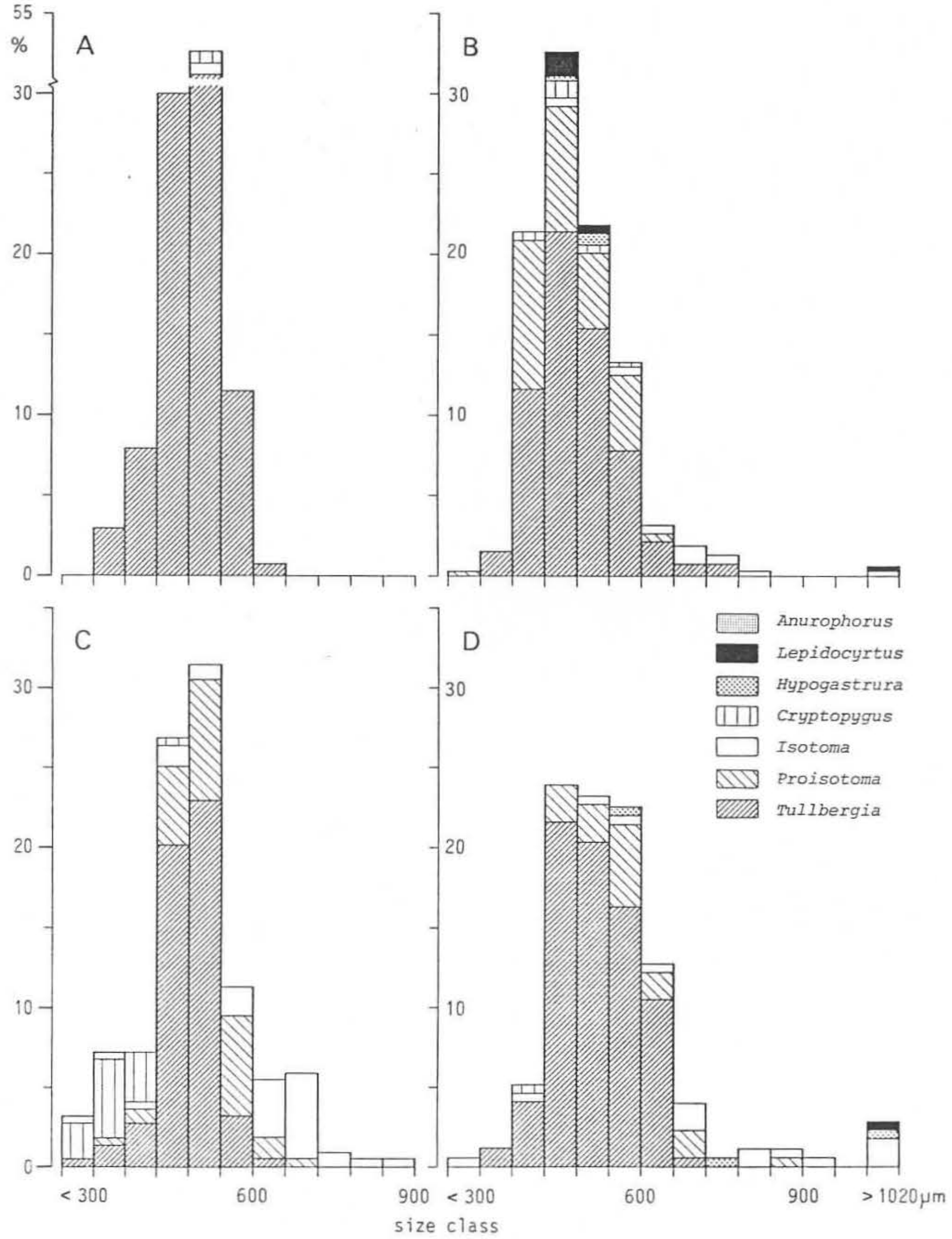

Fig. 2. Size class distribution of the Collembola species found in the two layers of the plots. A. without worms, 0–2.5 cm, B. with worms, 0–2.5 cm, C. without worms, 2.5–5 cm, D. with worms, 2.5–5 cm.

smaller than most pores in the habitat with the smallest pores so they would not be hampered by lack of space to move about. Still they were confined to the coarse gravel with large pores. Perhaps a direct relation between pore size and body size can not be expected for all length classes of mesofauna. HOLT (1981) found that only the distribution of small cryptostigmatic mites could be attributed to pores of comparable size. He suggested that these small animals needed the pores for protection against bigger predators, while big mites are much less susceptible to predation. Different thigmotactic reactions of various species could also be important.

In this study, other factors such as food availability may be important in addition to pore size distribution in determining living conditions for Collembola. In the soil without earthworms, almost all organic material is confined to the root mat, which provides a readily available food source for the animals. In soils, with earthworms the organic material is distributed more homogeneously through the profile, forcing the Collembola to search for food deeper in the soil profile.

A very important factor controlling Collembola size distribution in the soil may be the direction and shape of the total pore system. Not all pores visible in the thin sections are accessible to the animals because they may not be interconnected. Unfortunately, the fraction of inaccessible pores cannot be assessed with the technique used. Because the pores in both layers of the soil without earthworms are mostly horizontally oriented vertical migrations of the animals may be hampered. So, during periods of abiotic stress, be it drought or frost, it may be difficult for the Collembola in the root mat to seek refuge in the mineral layer. Such populations may have to regrow regularly from inocula, such as for example eggs, that can withstand adverse situations. The relative small size range within the same species in the plot without earthworms, compared with the earthworm plot, could indicate that the population was recovering from winter losses.

5. Conclusions

Collembola tend to be larger in earthworm plots: individuals of the same species are larger in the plots with earthworms and some rather large species present here are absent in the soil without earthworms. The trend in body length of the Collembola relates to the higher numbers and larger cross-sectional area of bigger pores in the soil of the earthworm plot. However, Collembola sizes cannot be directly correlated to pore size distribution, the differences between the structure of the 2 plots referring mainly to pores wider than most of the Collembola.

In addition to pore size distribution and food availability, architecture of the pore system may be important. The horizontally oriented pore system and the concentration of food sources at shallow depth in the soil without earthworms seems to be less suitable for Collembola survival during adverse conditions: most of the animals are confined to the root mat layer. In the earthworm plot deeper layers of the profile are more readily accessible.

Studying pore size distribution by means of thin sections gives usefull information about some important characteristics of the habitat small animals like Collembola have to deal with. However, not only pore space should be measured, but also the architecture of the pore system should be taken into account. This can be done qualitatively, as has been shown in this study, but also quantitatively, by assigning pore size classes to different pore types. Therefore it is necessary to qualitatively describe pore types such as planes or channels by means of area/perimeter proportions. Also the interconnection of the different pores should be investigated in the thin sections. This can be done with for example the methylene blue method as described by BOUMA (1981).

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The influence of soil structure on Collembola was studied in a grassland plot, where soil structure was changed locally by earthworms. Without earthworms, a root mat with large horizontal pores, and a sharp boundary to the mineral soil was formed. The mineral soil showed only small, horizontally oriented pores. In the earthworm plot, pores were oriented in all directions, and also more macropores were present than in the plot without earthworms. *Tullbergia krausbaueri* was common in both plots to a depth of 5 cm. In the plot without worms *Isotoma notabilis, Proisotoma* sp. and *Cryptopygus bipunctatus* were present only in the root mat, while they were present to a depth of at least 5 cm in the worm plot. Collembola were generally larger in the worm plot, because (a) larger species were present and (b) individuals of most species were bigger than in the plot without worms. The number of pores of size classes large enough to contain collembola (30–800 μm) did not differ between the plots. The results of this study suggest that the predominantly horizontal pores in the mineral part in the plot without worms hampered the vertical movement of the Collembola, confining them to the root mat. As a result, Collembola populations in the plot without earthworms were probably more vulnerable to adverse temperature and moisture conditions. The distribution of food might be an additional factor influencing the depth distribution in both plots.

Key words: soil structure, architecture of pores, Collembola, size distribution, earthworms.

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